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Homing pigeons as a model for the influence of experience on brain composition-including considerations on evolutionary theory

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The brain of homing pigeons seems to be functionally adapted to homing with e.g., larger hippocampi and olfactory bulbs. Furthermore, functional lateralization occurs as well in homing pigeons. Recently, the investigation of the influence of navigational experience on brain composition and lateralization revealed larger hippocampi in homing pigeons with navigational experience compared to inexperienced homing pigeons. Additionally, there are several brain structures in homing pigeons that show a volumetrical lateralization, whereas homing pigeons with navigational experience show a more lateralized brain than pigeons without navigational experience. This gives more insights in the neuronal basis of orientation and brain development in general but demonstrates as well its complexity. Plasticity and lateralization are much more correlated with individual life history than assumed up to date and have to be more considered in comparative research of evolution.

In research on avian navigation, the homing pigeon (*Columba livia* f.d.) is a suitable model for investigating the mechanisms used by birds to find their way home from remote areas. Homing pigeons, as a domesticated species, show an excellent homing drive to their home loft, what facilitates the search for mechanisms that might be working in many species but cannot always be studied under the favorable conditions of domestication. All behavior has its origin in the brain and thus, homing pigeons are as well qualified for investigating the neuronal basis of homing or navigation and corresponding neuroanatomical particularities. The strong selection for excellent homing performance led to a functional adapted and characteristic brain composition. Thus, homing pigeons have e.g., larger brains in comparison to other non-homing pigeon breeds or their wild ancestor, the rock dove[1,2] and show some peculiarities like increased hippocampi or olfactory bulbs, which are both involved in homing.[2-4]

Particular the hippocampus attracts attention in a peculiar way, because it plays a critical role in processing spatial information not just in homing pigeons amongst the birds but also in mammals.[5-8] It is known that the avian hippocampus is plastic in response to migratory experience and food-storing experience[9-11] and recently, we could show that flying and navigational experience has an influence on characteristic hippocampus volume in homing pigeons.[12] This finding confirms the role of the hippocampus during navigation and indicates that experience is a precondition to full hippocampal development. Thus, the special behavior of homing pigeons allows us to investigate the influence of experience on brain composition in an easy way by comparing pigeons that were allowed to gain navigational experience with pigeons that were not allowed to make such experience (e.g., by staying permanently in the loft). Such studies show, that maybe it is time to reconsider the assumption of a mainly genetically determined brain (composition) with not much potential for experience based (individual) alterations.

Functional specialization of the left and right hemisphere ('lateralization') is topic of much actual research and occurs as well in homing pigeons.[13-15] In our recent study we could show, again with our above mentioned methodical approach, that there is not just a volumetrical lateralization in homing pigeons but as well that this lateralization is caused by experience.[16] Several structures in homing pigeons show a volumetrical lateralization, but homing pigeons with navigational experience show a more lateralized brain than pigeons without navigational experience. The comparison of left/right quotients of those pigeons reveal that experienced homing pigeons show a smaller left mesopallium in comparison to the right one and homing pigeons without navigational experience a larger left mesopallium in comparison to the right one. There are as well significant differences between left and right brain subdivisions within the two pigeon groups namely a larger left hyperpallium apicale in both pigeon groups and a larger right nidopallium, left hippocampus and right optic tectum in pigeons with navigational experience. These results offer new insights in the neuronal basis of not just homing behavior, but orientation in general and as well its development.

Additionally, these results show again, that plasticity in the brain is more extensive and complex than known up to date and that even the left or right part of a subsystem might follow different trends of alterations and could be influenced by experience. It seems to be, that both, brain size and brain composition (of both hemispheres) depends an individual demands of function.

Our findings indicate a mutual relationship between experience (life history) and brain part size. Obviously, this is not restricted to domestic animals, but also seen in the wild as has been shown by Clayton and Krebs.[9] Such insights might have an impact on evolutionary theory which argues consciously (or unconsciously) that a form-function correlation results from heritable traits which have been proven to be evolutionary advantageous in terms of adaptive selection. Some authors do not agree that adaptation act as a driving force in evolution. One of the leading authors is the late Stephen J. Gould. In his book,[17] which is a sort of a legacy, he argues thoroughly for his theory of punctuated equilibrium. The central idea is that innovation in evolution does not result primarily from adaptive selection and heritability of respective traits. Our findings suggest that non-heritable features gained by learning are of great adaptive value. Thus, our results would support the theory of punctuated equilibrium, because of a shown biological superiority that is not accompanied by heritability. However, we do not share this interpretation and refer to evolutionary game theory, which is widely ignored by Gould. It has been introduced by Maynard Smith[18] and is nowadays elaborated sophistically.[19] This theory is based on population genetics and scientifically extremely satisfying because it makes use of (objective) mathematics and can produce testable hypotheses.

The cornerstone of game theory is the term "strategy." A strategy might be a certain morphological, physiological or ethological trait that competes with another trait. By definition, winning the competition is due to a greater fitness that makes the F1 or the F2 generation superior in terms of generative power. In traditional terms this means that the strategy under focus is heritable. However, our data led us to propose that in case of brain anatomy such a strategy might be composed by a heritable part and a non-heritable part that is due to life history. The relevance of the life history part must be significant since a parent cannot pass his favorable genes to the next generation if their potential has not been fully displayed. If we assume a genetical predisposition for learning (or navigation)—as we do it for homing pigeons—it is necessary to make use of this genetical potential. Otherwise there would be no transfer to the next generation. In the framework of game theory we have to deal with a mixed strategy; one player may be able to make use of two strategies. Obviously the life history part has to be somewhat larger than the genetic proportion. It would be interesting to see how evolutionary game theorists would model this dual structure of strategy and whether they could find a model that predicts how large both parts should be to achieve the status of an evolutionary stable strategy.[18]

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